

Article

GPS tracking of non-breeding ravens reveals the importance of anthropogenic food sources during their dispersal in the Eastern Alps

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Abstract

In many songbirds, the space use of breeders is well studied but poorly understood for non-breeders. In common ravens, some studies of non-breeders indicate high vagrancy with large individual differences in home range size, whereas others show that up to 40% of marked non-breeders can be regularly observed at the same anthropogenic food source over months to years. The aim of this study was to provide new insights on ravens' behavior during dispersal in the Eastern Alps. We deployed Global Positioning System (GPS) loggers on 10 individuals to gather accurate spatial and temporal information on their movements to quantify: 1) the dimension of the birds' space use (home range size with seasonal effects and daily/long-term travel distances), 2) how long they stayed in a dispersal stage of wandering as opposed to settling temporarily, and 3) their destination of movements. We recorded movements of up to 40 km per hour, more than 160 km within 1 day and more than 11,000 km within 20 months, indicating high vagrancy. Switching frequently between temporarily settling and travelling large distances in short time intervals leads to extensive home ranges, which also explains and combines the different findings in the literature. The destinations are rich anthropogenic food sources, where the birds spent on average 75% of their time. We discuss how ravens may find these "feeding hot spots" and which factors may influence their decision to stay/leave a site. The strong dependence on anthropogenic resources found in this population may have implications for site management and conservation issues.

Key words: common raven, *Corvus corax*, non-breeder, space use, dispersal, kernel density.

The process of dispersal helps solving social conflicts coming from intraspecific competition, it reduces inbreeding, and it also helps individuals exploit new abiotic and biotic conditions (Baguette et al. 2014). Dispersal can also be costly in terms of energetics, time, risk, and lost reproductive opportunities (Bonte et al. 2012). It influences the fitness of the individual and affects population dynamic, species distribution, and genetics (Dunning et al. 1995; Clobert et al. 2001). Consequently, research on dispersal is important for population management and for predicting how populations respond to

environmental changes (Bowler and Benton 2005). Dispersal consists of 3 successive behavioral stages: 1) "emigration," when an individual leaves its birth place or temporary settlement; 2) "wandering" or "transience," an inter-patch movement to explore areas before settling in a new patch; and 3) "immigration," when individuals either stay in a breeding territory or in a temporary settlement (Bowler and Benton 2005; Delgado and Penteriani 2008; Clobert et al. 2009). The temporary settlement during dispersal reflects the transition from an exploratory strategy with incomplete

information to a more specific use of the spatial and social environment (Delgado et al., 2009) and can thus decrease costs of dispersal (Bonte et al. 2012). Very little is known about the behavior and intraspecific interactions of sexually immature and mature non-breeders (Penteriani and Delgado 2011).

The common raven *Corvus corax* is a species with a prolonged juvenile period and poorly understood movement patterns during their dispersal process. As breeders they are long-term monogamous and defend a territory year round, which is often larger than 10 km² (Haffer and Kirchner 1993; Rösner and Selva 2005). To become a breeder, sexually mature individuals have to find a partner and be able to defend a territory, which does not occur before they are 3–4 years old (Ratcliffe 1997; Webb et al. 2009) and, in some populations, may take up to 10 years or more (Loretto and Bugnyar, unpublished data).

In this early life stage, ravens are often found in groups for foraging and roosting (Haffer and Kirchner 1993; Ratcliffe 1997; Wright et al. 2003). These non-breeder groups can be highly vagrant (Heinrich et al. 1994), but their members may also develop preferences for certain foraging sites (Braun et al. 2012). Whereas breeders share only little space with their neighboring breeding pairs, the non-breeders have overlapping home ranges especially when they aggregate at food sources or roosts (Heinrich et al. 1994; Marzluff and Neatherlin 2006; Webb et al. 2012; Scarpignato and George 2013). Ephemeral food sources such as carcasses or road kills may attract large numbers of ravens (Heinrich 1989; Marzluff et al. 1996; Stahler et al. 2002), and permanent anthropogenic point subsidies such as farms, landfills, or game parks do so even more (Huber 1991; Drack and Kotrschal 1995; Boarman et al. 2006; Powell and Backensto 2009; Webb et al. 2012; Bijlsma and Seldam 2013). In a review of North American studies, Boarman and Heinrich (1999) report home range sizes from 1.20–1,252 km² for non-breeding ravens, a huge variation that could reflect regional differences, different resource distributions, or population densities. Most studies used a mark-recapture design (observations of rings/wing tags, recovery of dead ravens) or radio telemetry, which requires a huge effort during data collection especially when a high temporal resolution is desired.

In contrast to North America, only few studies on ravens' space use have been carried out in Europe. In the Swiss Alps, Huber (1991) reported movements between food sources of up to 30 km. In the northern Austrian Alps, the presence and absence of marked ravens (mainly non-breeders) has been monitored at a regular food source since 2008; results show that about 40% of the marked birds use the site almost on a daily basis over months and even years, whereas the other 60% visit the area infrequently or even just once (Braun et al. 2012). In the same population, the formation of social bonds and regular interventions in bonding attempts of conspecifics have been observed; as forming bonds facilitates access to resources (Braun and Bugnyar 2012), interventions in others' bonding attempts have been interpreted with preventing them from becoming strong competitors (Massen et al. 2014). Results from captivity support these data, with social bonding starting in the first fall (Loretto et al. 2012) and bonded partners engaging in forms of post-conflict affiliation (Fraser and Bugnyar 2010; Fraser and Bugnyar 2011), indicating sophisticated relationship repair and support mechanisms.

Taken together the literature shows large variability during dispersal of ravens across areas and studies. It seems that some stay in a certain area, i.e., show long-term temporary settlement before breeding, and likely take advantage of being familiar with their

spatial and social environment; others remain in a wandering stage and thereby may explore new habitats and reduce intraspecific competition for resources. The aim of our study was to provide new insights about movement dynamics of non-breeding ravens in the Eastern Alps. We used GPS loggers to gather accurate spatial and temporal information on their movements and were specifically interested in: 1) the dimension of the birds' space use (home range size with seasonal effects and daily/long-term travel distances), 2) how long they stayed in a dispersal stage of wandering as opposed to settling temporarily, and 3) their destination of movements.

Materials and Methods

Study animals and tagging

We trapped wild ravens in the Cumberland Wildpark (47.804783°N, 13.947862°E), a game park located in the Almtal, a narrow valley in the northern Austrian Alps. This valley has its lowest elevation at around 500 m above sea level, surrounded by peaks of up to 2,515 m, and below the timberline it is mostly covered by forest. Depending on the season, 15 (summer) to 120 (winter) wild ravens scrounge food from the captive animals in the game park. During October 2012 and November 2013, we caught 10 ravens with drop in traps (built after Stiehl 1978) and outfitted them with backpack-mounted (Buehler et al. 1995) GPS loggers (model Duck 4C, Ecotone Telemetry, Poland; www.ecotone.pl), which weighed 30 g and never exceeded 3% of a bird's body weight (Millsbaugh and Marzluff 2001). The loggers have a solar panel with rechargeable batteries, and data are transmitted via the Global System for Mobile Communications (GSM) network. According to the manufacturer, 80% of the GPS fixes are at least within 20 m accuracy (but usually have far higher accuracy), which is consistent with our experience. The interval settings can be changed flexibly between 30 min and 24 h, depending on the battery level. Because ravens are diurnal birds, we aimed to use 1-h intervals, starting before sunrise until after sunset, to also include the night roost. However, some loggers did not perform as well as others, and bad light conditions, especially combined with short winter days, often only allowed larger sampling intervals (several hours or sometimes days). In this study, we analyzed all data collected until end of November 2014 (Table 1). Sex could be reliably determined from blood samples taken during the tagging procedure. Age class was assigned based on mouth and feather coloration as follows: juveniles (within their first year), subadults (second and third year), and adults (older than 3 years) (Heinrich and Marzluff 1992; Heinrich 1994a). The final sample included 5 males and 5 females from which 2 we tagged 2 as juveniles, 7 as subadult, and 1 as adult. Note that a large fraction of this study population is already sexually mature but still not breeding.

Data analysis

For each individual, we estimated the utilization distribution (UD), i.e., the probability where an animal occurs at any randomly chosen time (Worton 1989; Powell and Mitchell 2012). We used a fixed kernel density estimation and the plug-in method to select the smoothing parameters (Wand and Jones 1995) with the "ks" package (Duong 2007) in the program R (R Development Core Team 2014). The plug-in method has been shown to be more reliable than the traditionally used methods ("first generation" methods such as, e.g., least-square cross-validation) (Jones et al. 1996), even more so in its unconstrained version (Duong 2007). The areas within the 95 and 50% contours of the estimated UD were defined as home range and

Table 1. General information about tagged individuals (ID), mean/maximum number (#) of fixes per hour/day, percent of days in settling phase and calculated home range sizes with Kernel density estimation (UD), and MCPs are presented

ID	Fledged in	Sex	Date of tagging	Last GPS fix	No. of days with data	No. of GPS fixes	Mean no. of fixes per day	Max. distance/hour	Mean distance/day	Max. distance/day	Percentage of days settling	95% UD	50% UD	95% MCPs	50% MCPs
1 ^a	2007	f	19 October 2012	05 February 2013	110	828	7.53	4.33	8.64	23.93	97.27	1.2	0.1	18.3	0.9
2	2010/2011	f	20 April 2013	30 November 2014	253	830	3.28	10.05	7.75	75.46	89.33	37.8	1.7	112.3	8.0
3	2012	f	29 March 2013	30 November 2014	342	1,780	5.20	17.94	8.52	73.90	86.84	129.9	2.1	4,032.9	595.2
4	2012	f	14 April 2013	30 November 2014	594	6,517	10.97	43.56	20.04	144.50	69.53	1,732.6	25.6	1,8833.1	11,798.6
5 ^b	2013	f	01 September 2013	24 April 2014	235	1,969	8.38	13.33	3.67	31.65	98.72	0.9	0.1	6.4	0.4
6 ^c	2011/2012	m	16 November 2013	30 November 2014	378	4,938	13.06	39.29	15.95	140.20	75.13	163.0	7.2	2,097.2	1,394.4
7	2012	m	03 September 2013	30 November 2014	374	2,636	7.05	22.8	21.63	109.80	40.91	80.0	5.2	614.5	37.8
8	2012	m	31 October 2013	30 November 2014	393	4,347	11.06	35.87	21.3	164.30	59.03	1,206.9	44.8	8,100.7	4,948.3
9	2012	m	15 November 2013	23 June 2014	220	2,286	10.39	35.13	14.01	137.80	78.64	21.6	0.42	459.0	1.2
10 ^d	2013	m	16 August 2013	23 January 2014	161	1,507	9.36	10.22	2.04	28.60	98.14	1.6	0.08	84.4	1.3

^aLast signal from a slope with high risk of avalanches; individual has not been observed since.^bGPS logger, wing tag, rings, and some feathers were found in an wild boar enclosure.^cGPS logger failed, individual was observed almost daily during the rest of the study period.^dRaven removed the GPS logger and was regularly observed during the rest of the study period.

core area. To understand the reason for the intensive use of certain areas, we identified night roosts, based on the times of the fixes, and food sources, e.g., farms, compost stations, garbage dumps, identified by satellite images and maps, within the 50% core areas of each individual. In order to compare our data with other, especially older, studies using different home range metrics, we also calculated the minimum convex polygons (MCPs) for each individual (95% as home range and 50% as core area) using the “adehabitat” package (Calenge 2006).

Additionally, we divided all data according to the astronomical seasons (March 21, June 21, September 23, and December 21). For each individual and season with a minimum sample size of 20 GPS fixes, we calculated the 95% UD and tested which factors influence the size of these areas by created generalized linear models (family = gamma, link = logit) with the following fixed factors: season (4 meteorological seasons), number of GPS fixes, year of data collection, sex, and as random factor the individuals' identity. We used a multi-model inference approach, calculating all possible fixed-effect model combinations and recorded their Akaike information criterion corrected for small sample sizes (AICc). We then ranked all models according to their AICc values and selected the models with a $\Delta AICc < 2$ from the top-ranked model for model averaging in order to create model-averaged coefficients (Burnham and Anderson 2002). To investigate coefficient level differences, we then used the Tukey test for multiple comparisons in parametric model from the package “multcomp.”

To describe the ravens' movements, we calculated the maximum distance per hour, the maximum and average distance per day, using the cumulative Euclidian distance between the first position on 1 day and the first position of the consecutive day. This procedure allowed including potentially missed movements from sunset to sunrise and excluded days without data collection due to low battery level. For the total travelled distance, the cumulative Euclidian distance between all points during the period of data collection for each individual was computed.

To judge whether an individual was wandering or settling temporarily, we defined a threshold that assigned each day either to the wandering or the settling phase, depending on the distance travelled. If such a threshold is set low, most days would be defined as “wandering,” while a high threshold (e.g., 50 km/day) would define most days as settling temporarily. We iteratively calculated the proportion of days in the wandering phase, starting at 0 m and increasing by 100 m up to a maximum of 50 km, which represents roughly 95% of the data (Figure 1). We then fitted a model with an exponential decay function including a multiplicative and an additive term

$$y = a + b * e^{c * x}$$

to these points and calculated the value of the threshold point, where the slope of the tangent is 45° (Supplementary Figure A). This indicates the point on the curve where a 1% change on the x-axis equals a 1% change on the y-axis, thus representing the optimal trade-off point on a Pareto boundary (Van den Berg and Friedlander 2008). This threshold point was then used to separate settlement from wandering behavior for each day and individual. Then we calculated how many days on average and at maximum the individuals stayed in which stage. We borrowed the threshold point definition from applied mathematics where it can be used to solve multi-objective optimization problems. In our case, we used it to define a mathematical separation of settlement and wandering; however, this

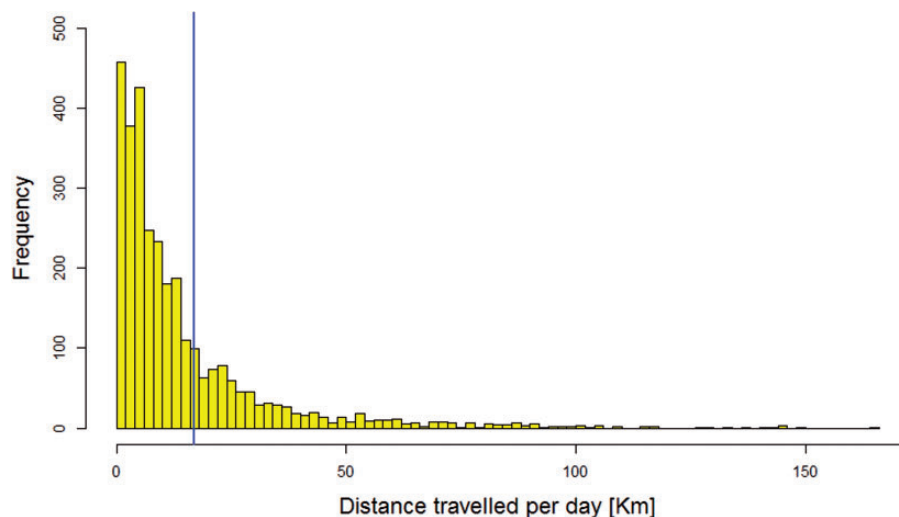


Figure 1. Histogram of the daily travel distance. The calculated threshold between the settling and wandering stages is shown in blue at 16.88 km.

method should be used with caution, because the different GPS sampling rates might affect the cumulative distance.

Additionally, we calculated the net squared displacement (NSD) and plotted the associated graphs using the function *ltraj* in the “adehabitat” package (Calenge 2006) in Supplementary Figure B. The NSD measures the straight line distance between the starting location and subsequent locations for the movement path of an individual (Bunnfeld et al. 2011). This statistic is fundamental for quantifying movements of organisms as it provides key properties of movement paths (Turchin 1998) and can be used to distinguish between different movement patterns, e.g., migratory stationary animals (Turchin 1998; Bunnfeld et al. 2011; Myrsetrud et al. 2011; Killeen et al. 2014).

Results

Space use of non-breeding ravens

In our analysis, we included 27,638 GPS fixes of 10 ravens during an average of 306 days per individual (110–594 days) (Table 1). The maximum calculated flight distance per hour was 43.56 km, the overall average distance flown per day was 12.36 km (individuals’ averages ranged from 2.04 to 21.63 km), and the longest distance flown within 24 h was 164.30 km (Table 1). The data reveal that ravens can fly more than 11,010 km over 594 days (roughly 20 months). Because our tracking interval was at best 1 GPS position per hour, but often much lower, these values are still rather conservative estimates. The home range sizes, calculated as 95% of the UD of the 10 non-breeding ravens, ranged from 0.86 to 1,732.57 km² and the core areas (50% UD) had an estimated size of 0.06 to 44.84 km² (Table 1, Figure 2 and Supplementary Figure C). The MCPs were in general about an order of magnitude larger and encompassed many areas that may have never been used by these individuals (Table 1 and Figure 2).

Splitting up the data per individual and season resulted in 45 home range estimations (95% UD) from 10 individuals. The best model explaining the size of the 95% UD had the individuals’ identity as random factor and season as fixed factor, whereas sex, number of GPS fixes, and the year of the season did not improve the model. Thus, season seems to be the most important factor influencing changes in ravens’ movements. Home ranges were largest in

winter with a difference to spring ($P < 0.001$) and in comparison with summer ($P = 0.053$).

There are positive correlations between the size of the home range and the mean and maximum distance travelled per day (mean distance: $R^2 = 0.68$, $P = 0.035$, $n = 10$; maximum distance: $R^2 = 0.84$, $P = 0.005$, $n = 10$; Spearman rank correlations), indicating that those individuals, who cover large areas also move around far and fast. We found a positive correlation between the sample size of GPS fixes and the home range size over the whole tracking period (Spearman rank correlations: 95% UD, $R^2 = 0.79$, $P = 0.010$ and 50% UD, $R^2 = 0.78$, $P = 0.007$). Thus, even with this high number of measured relocations during up to 20 months a home range cannot clearly be defined most likely due to frequent changes in space use.

Wandering or temporarily settling

The threshold between wandering and temporarily settling was calculated at a daily travelling distance of 16.88 km (Figure 1). On average, the ravens remained in a given location for 19.52 days with movements under the specified threshold, with a recorded maximum of 145 consecutive days. The wandering phase was comparatively short, on average 2.25 days, with a maximum of 33 consecutive days spent moving beyond the threshold. In total, individuals spent 74.35% of the sampling period (3,060 raven days) in a temporary settling phase. Per individual the proportion of all days settled is negatively correlated with their home range size (Spearman rank correlations: 95% UD, $R^2 = -0.78$, $P = 0.012$ and 50% UD, $R^2 = -0.87$, $P = 0.001$), indicating that local birds stay at the same location, whereas vagrant birds regularly switch between different areas.

In Supplementary Figure B, the NSD for each individual over its sampling period is shown. The figures support the findings that wandering stages are rather short in comparison with settlement (i.e., when NSD is on the same level).

Destinations of the movements

The core area (50% UD) of 6 individuals was encompassed by 1 single polygon, whereas 2–6 polygons represented the core area of the other 4 individuals. These 4 individuals also had the highest number of GPS fixes and days with data collection. Interestingly, we identified in 18 of these polygons a permanent anthropogenic food source and in 2 cases a night roost, i.e., the area was mainly used from dusk until dawn. Out of these anthropogenic sources, 8 were game parks or

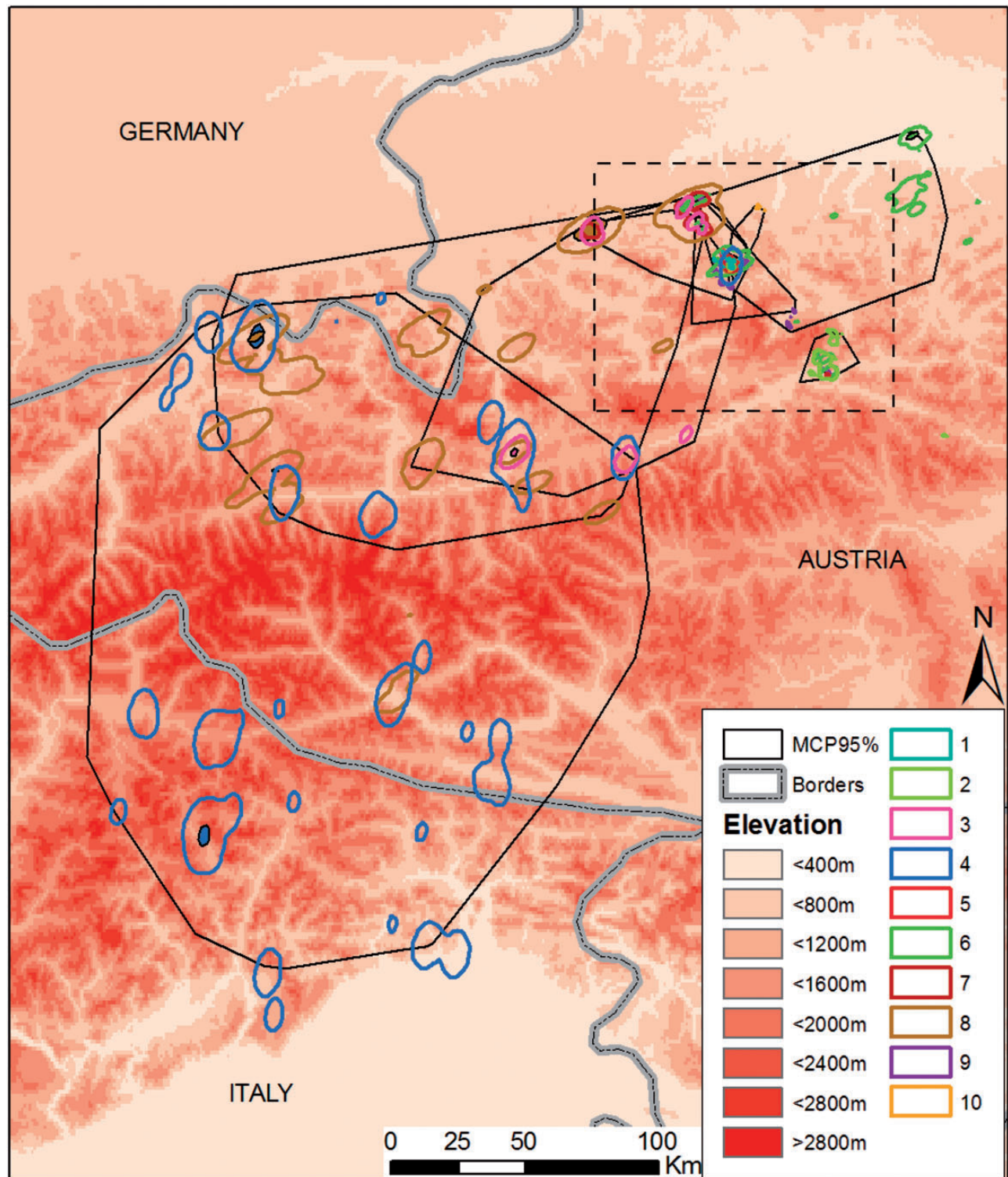


Figure 2. Spatial distribution of 10 GPS tagged ravens in the eastern Alps. The coloured polygons represent the different individuals' 95% UD and as filled areas the 50% UD. The black polygons show the 95% MCP. The dashed area with the trapping site in its centre is enlarged in the [Supplementary Fig. C](#).

zoos and 10 were garbage dumps or composting sites. In winter, ravens also spent much time in skiing areas moving between huts to scavenge kitchen leftovers, but due to the seasonality of this foraging it is not represented in the core areas over the whole sampling period.

Overall, we found no differences between males and females in any of the investigated variables (5 males, 5 females, Wilcoxon test) nor an indication that body weight measured on the day of tagging had any influence.

Discussion

Space use of non-breeding ravens

This is the first study on space use of non-breeding ravens with a high temporal accuracy carried out over up to 20 months. Our data are collected during the wandering stage of ravens' dispersal and show movements of more than 40 km per hour, more than 160 km within 1 day and more than 11,000 km within 20 months. However, most of the time these individuals settle temporarily near anthropogenic food sources and switch between these or new areas, leading to an average home range size of 337.53 km² (max: 1,732.57 km²) when calculated with kernel density estimation. For some individuals, the travel distances and the home range sizes are surprisingly extensive, compared with Eurasian Griffon vulture *Gyps fulvus* non-breeders, a much larger scavenger species that also has a prolonged juvenile period and relies on thermal and orographic uplifts for soaring flights to cover long distances (Ruxton and Houston 2004). In a study with a similar sampling rate (1 GPS fix/hour), the maximum distance travelled per hour was 48.38 km, 119.98 km per day, and the median home range size was 4078 km² (95% UD) (García-Ripollés et al. 2011).

To our knowledge, such extensive movements in very short time (hour/day) have not previously been reported for ravens. Also, the maximum home range size of these non-breeders calculated as MCP (18,833.14 km²) is far more wide-ranging than those reported in previous studies (1.20–1,252.00 km², see, e.g., Boarman and Heinrich 1999). As has been discussed in the literature, the home range sizes can differ considerably depending on the estimation method used (e.g., Fieberg and Börger 2012). In our case, calculating the UDs results in smaller home ranges, which, however, are more useful when trying to predict with a 95% probability in which area a specific individual can be found. Thus, differences in the home range size between studies might reflect differences concerning the region, the resources distribution, the population density (Boarman and Heinrich 1999), but also different sampling methods and analysis techniques. In particular additional “noise” can arise, when the home range does not approach an asymptote computed with kernel density estimation (Laver and Kelly 2008), in other words there are not enough sampled positions to describe the entire home range. According to this in the strict sense for most if not all individuals, our sampling period was too short to fully describe their home ranges which is further supported by a positive correlation between the individuals' home range size and the number of GPS fixes. Thus, even though our home range estimates are larger than those in the literature, they might still be underestimated. The necessity of such long sampling periods suggests constant exploration and wandering during the dispersal of non-breeding ravens. Therefore, we question the relevance and informative value of an estimated home range, including the choice of the analytical method for such cases. In some systems, other movement or usage-based metrics than home range estimators might be worth considering (Fieberg and Börger 2012). We stress this argument especially for highly vagrant species or life stages of a species, where, e.g., travel distance per hour, day, and year, seasonal differences as well as how long an animal stays in a certain area, might be more informative than only estimated home range metrics.

The positive correlations between mean and maximum distance travelled per day and home range size might seem trivial; however, individuals could also move a lot within a rather small range. Still these results have to be taken with caution, because the sampling rate can strongly affect the calculated distances. For the home range

estimates, we suggest the different sampling rates have less impact and cannot fully explain the individual differences (e.g., when comparing ID 6 and 8).

Seasonal home range differences

The seasonal comparison revealed that these non-breeding ravens use larger areas in winter than in spring and summer. Importantly, the number of fixes per season did not improve the model; therefore, we here conclude that the sampling interval plays a minor role in this aspect. These results are in contrast with those found in another scavenger species; Monsarrat et al. (2013) found that Griffon vultures in France have the smallest home ranges in winter and the largest in spring. Most likely the short day length and limited thermal soaring in winter forces them to concentrate their activity around rich and predictable food sources (e.g., feeding stations) leading to high intraspecific competition, whereas in spring and summer with optimal flight conditions they use larger areas allowing them to reduce this intraspecific competition (Monsarrat et al. 2013). At least in our study site, the intraspecific competition for ravens is also much higher in winter than in summer. In particular, with snow cover, food is scarce though ravens as well as vultures prefer predictable food sources, but ravens might depend less on the flight conditions (especially thermals) than the much larger and heavier vultures. Furthermore, we found that in winter, ravens intensively use skiing areas where they visit several Alpine huts presumably to scavenge kitchen leftovers. These small but also predictable food sources are spread out over large areas and are used in addition to larger permanent food sources and lead to larger home ranges. Potentially, this is a pattern rather similar to more natural situations, less densely populated by humans, where ravens preferentially associate with wolves (Stahler et al. 2002) and might even have an impact on kill rates (Kaczensky et al. 2005) and group sizes of these predators (Vucetich et al. 2004).

Wandering or temporarily settling

Despite our small sample size, the results provide a clear indication that temporary settlements are common within non-breeding ravens of the Alpine population. Around 75% of their time, the birds did not move further per day than our calculated threshold. This could either be due to the fact that they are moving very slowly across the landscape or, more likely, staying within 1 area. We found that settling phases usually consisted of more consecutive days than wandering phases. The threshold is an artificial construct, but the histogram of the ravens' daily travel distances (Figure 1) supports it and shows that most flights are within a short range and very long flights are rare. Even though these numbers might be underestimated for animals with lower sampling rates, the pattern of shorter wandering phases versus longer periods in the same distance to the capture site is also visible in the NSD plots in Supplementary Figure B. Further, this is in line with the results of a recent study on the space use of radio-tagged ravens around a permanent food source, which showed very high site fidelity at an anthropogenic food source (Loretto et al. 2015). A reason for this limited space use around food sources might be the highly territorial behavior of breeders, which dominate all individual intruders on their territory (Heinrich 1989). However, if there are too many non-breeders, as in the case at these food sources, non-breeders overcome the territorial defense (Marzluff and Heinrich 1991).

Destinations of the movements

To assess the most important destinations of movements over the whole sampling period, we focused on the estimated UD_s (the core areas of each individual, Figure 2 and Supplementary Figure C) and explored every frequently visited area. We found, apart from 2 night roosts, that all frequently used areas encompassed a permanent anthropogenic food source, confirming a large influence of human settlements on non-breeding ravens. Potentially, the dispersal of non-breeding ravens is even limited or influenced by their intensive use of anthropogenic food sources. This is supported by the idea of a cultural coevolution between humans and birds of the genus *Corvus* (crows and ravens) (Marzluff and Angell 2005) and most likely leads to higher non-breeder densities in certain areas with higher competition for territories than under conditions without human influence. At our study site, the area around the food source seems to be saturated by territories. Even though breeders frequently use this food source, they do not seem capable of defending it against non-breeders and other breeders. In other populations, a negative impact on the breeding success of the adjacent territorial pairs has also been documented and explained by increased territorial fights (Bijlsma and Seldam 2013; but see Marzluff and Neatherlin 2006).

Given that ravens move fast (short wandering time) between food sources, where they settle for extended periods, we suggest that they have an extensive knowledge about the area, possibly in the form of a mental map (Tolman 1948). Whereas ephemeral resources such as skiing huts or small compost stations are limited by daytime and season, others such as zoos and garbage dumps exist year round and will therefore attract a higher number of ravens continuously. Learning about these opportunities, either individually or socially by following others (Heinrich 1988), seems crucial for Alpine ravens in the non-breeding state. Whether they stay at a site or continue the dispersal may depend on several, mutually not exclusive factors. For adults, it is probably most critical to find suitable partners and/or available territories. Individual differences in personality style and temperament may also play a role: some individuals may be more explorative and/or more prone to form routines than others (see Cote et al. 2010 and references therein). Finally, social integration and the ability to manage conflicts could determine an individual's preference for an area. When feeding in a group, aggression rates in ravens are typically high (Heinrich 1994b). If group formation occurs at a regular or permanent food source, as for all the cases identified here, socialized subgroups, rank hierarchies and social bonds can emerge (Braun et al. 2012; Braun and Bugnyar 2012), which might lead to a variety of social challenges. High aggression rates, lack of social allies or simply the fact that other members of a subgroup leave an area might affect how long a raven stays at a given site.

Taken together, we found that non-breeding ravens in the Austrian Alps frequently move between regular feeding “hot spots” that are of anthropogenic origin. These findings support the idea of a cultural and opportunistic adaption to the availability of human food sources (Marzluff and Angell 2005), and the management of these sites may become important for conservation. We suggest that future projects should focus especially on the questions why and when individuals change their dispersal stage (wandering, settling) emphasizing the link between movement, personality, and social aspects. This would allow comparing the social structure and fission–fusion dynamics of a highly cognitive bird species with similar cognitively advanced mammals (Silk et al. 2014) and may increase our understanding of the evolution of social behavior.

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Supplementary Material

Supplementary material can be found at <http://www.oxfordjournals.org/>.

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